

form *T. sipylus*, clearly proving this to be a well-marked geographical race distinct from *T. evenina*.

An example of what seems to be an intermediate phase of *T. vesta*, differing from the wet-season form of *T. mutans* in its small discocellular black spot, smaller discal salmon-buff spots, larger marginal spots, and strongly defined brown bands on the under surface of the secondaries.

A form which I take to be a dry-season phase of *T. ansorgei*, already referred to in footnote.

Specimens of *Herpænia melanarge* showing considerable variation in size, proving that *H. iterata* (which differs constantly in the red coloration of the markings below) is a nearly allied but distinct geographical race.

Lastly, examples of *Papilio erinus* with unusually narrow blue banding on the upper surface of the primaries.

4. On the Malagasy Rodent Genus *Brachyuromys*; and on the Mutual Relations of some Groups of the *Muridæ* (*Hesperomyiæ*, *Microtinæ*, *Murinæ*, and "*Spalacidæ*") with each other and with the Malagasy *Nesomyiæ*.  
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(Plates XXXVII.-XL.)

It has been stated not long ago (1893), in a valuable Manual, that the Rodents are amongst the few exceptions to the rule, according to which the Malagasy Mammals belong to peculiar specifically Malagasy genera<sup>1</sup>. This statement, made originally by Rüttimeyer in 1867<sup>2</sup>, was true at that date. In the intervening 28 years five genera, containing six species, of Malagasy Rodents have been brought to notice; several of them, however, were so scantily characterized as to explain the undue neglect to which they have been subjected.

The genus *Brachyuromys* was characterized by me last year<sup>3</sup>, upon specimens collected in Madagascar, the species *B. ramirohitra*, of which a short description was given, being taken as type. In the same place it was pointed out that Bartlett's "*Nesomys betsilcoensis*"<sup>4</sup> is a second species of *Brachyuromys*.

At this Society's Meeting of Dec. 1, 1896<sup>5</sup>, some considerations on the Malagasy Rodents as a whole were presented; the great majority of them I considered to "belong to the so-called Cricetine

<sup>1</sup> K. A. Zittel, 'Handbuch d. Paläontologie. IV. Vertebrata (Mammalia),' 1891-93, p. 767.

<sup>2</sup> L. Rüttimeyer, 'Ueber die Herkunft unserer Thierwelt. Eine zoogeographische Skizze.' Basel & Genf, 1867, p. 14.

<sup>3</sup> Ann. & Mag. Nat. Hist. ser. 6, vol. xviii, Oct. 1896, p. 322.

<sup>4</sup> P. Z. S. 1879, p. 770.

<sup>5</sup> P. Z. S. 1896, pp. 978-980.

group of muriform Rodents (*Muridæ*, auct.), of which they are the lowest of existing forms, having affinities with some of the least specialized of the family Dipodidæ, as defined by Winge, viz. with *Sminthus* and *Zapus*." It was further pointed out that the African and Asiatic *Rhizomyes* (*Tachyoryctes* and *Rhizomys*) present relations with the Malagasy Rodents, and that the affinity is especially close between *Tachyoryctes* and *Brachyuromys ramirohitra*.

In the present paper I propose to give a fuller description of the skull and dentition of the two species of *Brachyuromys*, and to compare them with those Rodents outside Madagascar with which, in my opinion, they have affinities. The description of the other Malagasy Muridæ must be postponed to a future paper; but I shall have to refer to them repeatedly in the following pages.

### Genus BRACHYUROMYS, Maj.

Skull broad and massive. Upper profile of cerebral cranium flattened. Supraorbital crests rounded off. Incisors and rooted semihypselodont molars ( $\frac{3-3}{3-3}$ ) large as compared to the size of the skull. Infraorbital foramen large, but on the whole with the shape characteristic of Muridæ. Jugal large and approaching the lachrymal. Transverse diameter of incisors exceeding the longitudinal<sup>1</sup>. Crowns of molars flattened, not tuberculate; unworn molars of species 2 half-tuberculate. In young specimens the crowns of the molars show three lobes of enamel, united by cement and obliquely disposed (inclining forwards with their outer portion), the posterior lobe in the upper, the anterior one in the lower molars being the smallest. These lobes soon unite together, producing various patterns, by which the different species may be easily distinguished. Tail shorter than usual in Muridæ.

By their broad, moderately flattened, roundish heads and comparatively short tails these Rodents recall somewhat the Voles in outer appearance.

1. BRACHYUROMYS RAMIROHITRA, Maj. (Plate XXXVII. fig. 2 and Plate XXXIX. figs. 1-3.)

Ears large, oval. Coloration of upper parts brown, abundantly mixed with black, on the sides less dark, the black hairs gradually diminishing. Lower parts fawn. Bases of hairs slate-coloured. Tail furnished above with black, beneath with grey hairs.

Parietal crests diverging anteriorly. Interparietal short in transverse, but longer in antero-posterior diameter than in *B. betsi-leoensis*. Molars very large, all about of equal size and pattern, the third in both jaws generally slightly smaller than the other

<sup>1</sup> (1) Where the incisors are wider than thick, the gnawing habit is feebly developed.—(2) Where the incisors are thicker than wide, the gnawing habit is greatly developed (Ryder, "The Significance of the Diameters of the Incisors in Rodents," Proc. Acad. Nat. Sci. Philadelphia, 1877, pp. 314-18).

two; the third upper one slightly triangular. The pattern presented by the uniting of the three enamel-lobes is as follows in moderately worn teeth. In the two anterior upper molars:— (1) an anterior enamel loop, open on the inner side and running obliquely across the crown, close up to the outer enamel margin of the tooth; (2) a posterior enamel islet, smaller in transverse extent than the anterior loop and almost parallel to it. In the last upper molar the anterior loop is shut out very soon from the inner side, so that this tooth presents two obliquely transverse enamel islets, with sometimes a third, smaller one, behind. In moderately worn lower molars the shorter anterior loop opens on the inner, the longer posterior loop on the outer side, the latter remaining open for a longer time than the former.

Dimensions in millimetres, those of the first two taken in the flesh:—

	Skin (M. 429), ♂. Type.	Skin (M. 509), ♂.	Spirit-specimen (M. 181), jun.
Length of head and body	165	162	c. 110
„ tail . . . . .	99	89	73
„ manus . . . . .	15	16	16
„ pes . . . . .	34	52	27
„ ear . . . . .	24	24	17

Dimensions, in millimetres, of the skull (M. 719, ♂):—basal length 32·5; length of nasals in middle line 13·5; length of frontals in m. l. 13·5; length of parietals in m. l. 6·3; interorbital breadth at narrowest 4·7; length of upper molar series 8·5; length of lower series 8·5; length of interparietal in middle line 5·2; breadth of skull between zygomatic arches 23·5.

*Loc.* Ampitambè Forest, Betsimisaraka country (on the border of N.E. Betsileo), 6 hours S.E. of Fandriana.—Ambohitombo Forest, Tanala country.

Native names *voalavoanala* (*i. e.* forest rat); *ramirohitra* (meaning probably: who goes in company, gregarious). Fossil in the lower deposits of the Children's Cave (Sirabè).

## 2. BRACHYUROMYS BETSILEOENSIS. (Plate XXXVII. fig. 1 and Plate XXXIX. figs. 7, 8.)

*Nesomys betsileoensis*, Bartlett (P. Z. S. London, 1879, p. 770).

Resembling *B. ramirohitra* in outer appearance, but smaller. The brown of the upper parts of the previous species gives place here to fawn, which, together with the black hairs, gives to the upper part of the fur almost an olivaceous colour.

Skull resembling that of *B. ramirohitra*, but parietal crests nearly parallel; interparietal longer in transverse, shorter in longitudinal diameter. Molar teeth absolutely, as well as comparatively, smaller than in *B. ramirohitra*, though large as compared to Muridæ in general. Third upper molar small. Enamel loops of all the molars slightly less oblique than in the

preceding species. The anterior one in upper, the posterior one in lower molars being divided in the middle of the crown at an early stage of wear, the pattern presented in middle-aged specimens is the following:—a single enamel loop opening on the inner side of upper and on the outer side of lower molars; two on the outer side of upper and the inner side of lower molars. The single loops on the inner side of upper and on the outer side of lower molars remain open for a longer time than the others.

Dimensions in millimetres, taken in the flesh:—

	Skin (M. 516), ♀. Type.	Skin (M. 625), ♀.	Skin (M. 628), ♂.
Length of head and body	142	145	125
„ tail . . . . .	89	94.5	68
„ manns . . . . .	12	13	11
„ pes . . . . .	28	27.5	25.5
„ ear . . . . .	17.5	20	17
Breadth of ear . . . . .	—	18	15.5

*Loc.* Ampitambè, outside the forest. Vinanitelo, close to the forest of the Independent Tanala of Ikongo, thirty miles south of Fianarantsoa. The specimens measured are from the former locality. Fossil in the Children's Cave near Sirabè; abundant in the superficial, very rare in the lower deposits.

*The Affinities of the Genus Brachyuromys with Tachyoryctes, Rhizomys, Spalax, and Siphneus.*

1. *Tachyoryctes* and *Rhizomys*.—With regard to the affinities of *Brachyuromys*, I made on a former occasion<sup>1</sup> the following statement:—“The African and Asiatic *Rhizomyes*, usually classed in the *Spalacida*, but which Winge places amongst the lowest *Murida*, alongside with the Tertiary *Cricetodon* and *Eomys*, are nearly related to the Malagasy group of Rodents by means of the Abyssinian *Tachyoryctes* (*Rhizomys*) and the Malagasy *Brachyuromys*, the former being but a very specialized fossorial form of the more generalized *Brachyuromys ramirohitra*. The molars are almost identical in both, only slightly more hypselodont in *Tachyoryctes*.” (They are much more so in the latter than in the former.) “If we divest the *Tachyoryctes* skull of its [excessive] fossorial characters and of the consequences of the more hypselodont molars, we obtain a *Brachyuromys* skull. Likewise the skulls of the young *Tachyoryctes* bear much greater resemblance to *Brachyuromys* than the adult. There is further a great correspondence in external characters if we disregard the smaller ears and eyes of *Tachyoryctes* and its fossorial claws.”

In the following I give the reasons for the above statements.

In spite of all the differences of the skulls at first sight, a closer

<sup>1</sup> P. Z. S. 1896, p. 979.

examination shows that the *Rhizomyes* (*Tachyoryctes*, *Rhizomys*) and *Brachyuromys* are nearly related to each other—the same holds good, in a somewhat minor degree, with regard to *Spalax* and *Siphneus*. The *Rhizomyes* are highly adapted to fossorial habits; *Brachyuromys* much less. The molars of both will be considered below.

The skull of the two (*Rhizomyes* and *Brachyuromys*) presents the following agreements, *B. ramirohitra* being somewhat intermediate between *Tachyoryctes* and *B. betsileoensis*, although standing of course closer to the latter:—

(1) The zygomata diverge outwards posteriorly, more in *Rhizomyes* than in *Brachyuromys*; the malar process of the squamosal parts at right angles from the skull and is strongly developed.

(2) The jugal is very strong and approaches closer to the lachrymal than in other Muridæ.

(3) The infraorbital foramen in *Brachyuromys* is situated higher above the molar series and reaches higher up than in other Muridæ; the narrowed lower portion being lower and wider in *B. ramirohitra*. In *Tachyoryctes* it is located higher still, and there is almost no narrowed passage below. In *Rhizomys* the foramen is situated higher still, and much shortened as well as broadened.

(4) The skulls of both *Rhizomyes* and *Brachyuromys* are depressed and massive.

(5) Mandibulæ short, massive and high. Anterior margin of coronoid process almost vertical.

(6) The lower maxillary border, between premaxillary suture and first molar, viewed in profile, appears higher anteriorly, sloping down backwards towards the anterior alveolar border.

(7) The molar series diverge backwards.

(8) The glenoid fossa is, outside and inside, delimited by longitudinal parallel crests.

(9) The anterior margin of the nasals does not reach as much forwards as that of the premaxillaries.

The skull of *Rhizomyes* differs from *Brachyuromys* in the following characters, which are all of them the expression of the higher fossorial adaptation and the more hypselodont molars:—

Eyes and ears very small; tail very short.

A sagittal crest. Increase in vertical extent of the maxilla, upwards as well as downwards.—Anterior narial aperture depressed and broad.—Foramina incisiva small and situated backwards, being overgrown by the premaxillaries. The upper posterior processes of the premaxillaries extend also far backwards.—The distance between m.1 and anterior extremity of the premaxillaries, depending on the increased length of the incisor alveoli, is much increased as well.—Viewed in profile, the sloping backwards of the inferior border of premaxillary and maxillary, between the incisors and first molar, is much steeper than in *Brachyuromys*.—The great horizontal extension of the lower incisors and the great vertical extension of the lower molars

produce the well-known changes in the shape of the mandibula.—The angular process is less curved inwards than in the Malagasy genus.—Occiput inclined forwards.

*Basis cranii.*—In *Brachyuromys* we have the conditions normal in Muridæ; the tympanic bones are remarkable for their small size. *Rhizomyes*: Auditory meatus tubular. The space behind the choanæ, whose base is formed by the basisphenoid, is much compressed laterally. Braudt, in his description of the skull of the genus *Rhizomys*<sup>1</sup>, comprehending both *Tachyoryctes* and *Rhizomyes*<sup>2</sup>, makes a statement apt to be misleading. Referring apparently to the figure of "*Nyctocleptes dekan*" (= *Rhizomys sumatrensis*) by Temminck,<sup>3</sup> he says:—"Die innern Flügelfortsätze des Keilbeins divergiren so stark nach aussen, dass hinten, wie bei keiner andern der bekannten Spalacoiden-Gattungen, eine sehr breite Gaumenrinne entsteht." All depends what extension is given to the term '*Gaumenrinne*' (palatal groove). The internal pterygoid processes in fact diverge much with their inferior borders, so that, as is shown in Temminck's figure, and in Pl. XXXVIII. fig. 3 of the present paper, they almost completely cover the pterygoid fossæ. Upwards, however, they converge very much; and lastly, in the upper third of their height, they run parallel with each other, so as to delimit a groove—whose bottom (or roof) is occupied by the basisphenoid—which is very deep anteriorly and whose upper portion is exceedingly narrow (*Rh. sinensis*). In *Rh. sumatrensis* the groove is slightly shallower and less narrow; and the same, although in a minor degree, holds good with regard to *Rh. pruinus*. In *Tachyoryctes* the groove in question is less deep; backwards, where it is no more bordered by the internal pterygoid processes, it appears as a very narrow longitudinal groove in the middle line of the basisphenoid, which is thus partitioned in two lateral portions; whereas in *Rhizomys* it has only somewhat raised borders. Anteriorly, the "palatal groove" appears somewhat deepened and enlarged, as shown in Rüppell's plate<sup>4</sup> and in Pl. XXXVIII. fig. 3 of the present paper.

In consequence of the vertical extent of the maxillary in *Rhizomys*, the bony palate comes to be situated at a very deep level. As a consequence, the external pterygoid processes also acquire a considerable vertical extension, since they serve as a "support for the maxillary."<sup>5</sup> But this is not the only explanation of the great depth of the pterygoid fossæ; otherwise their roof—or rather their bottom, as we are speaking of them as '*fossæ*'—would remain on a level with the inferior basis of the intervening basisphenoid. In *Rhizomys* and *Tachyoryctes* the anterior portion of the basisphenoid becomes increased in vertical size, forming a septum

<sup>1</sup> J. F. Brandt, "Untersuchungen üb. d. craniolog. Entwicklungsstufen d. Nager d. Jetztzeit," Mém. Acad. St. Pétersbourg, [6] ix. vii. 1855, p. 817.

<sup>2</sup> *Ib.* p. 306.

<sup>3</sup> 'Monographies de Mammalogie,' ii, Leiden, 1835, p. 40, pl. xxxiii. fig. 5.

<sup>4</sup> Mus. Senckenberg. iii. Taf. x. fig. 2c (*Rhizomys* [*Tachyoryctes*] *macrocephalus*).

<sup>5</sup> Winge, Meddel. Naturh. Foren. 1881, p. 40.

between the two pterygoid fossæ, which is reduced to a thin transparent plate.

In this way is brought about the great depth and spaciousness of the pterygoid fossæ. Their roof is covered by an irregular network of raised ridges, apparently for the pterygoid internus, greatly developed as a masticatory muscle.

A beginning of these conditions we meet with in the *Microtinae*: in *Fiber* there is in the bony septum a spacious fenestra, situated farther backwards than the small fontanelle which is seen in *Tachyoryctes*. The *Microtinae* are somewhat intermediate in this respect between the *Rhizomyes* and typical brachyodont Muridæ, including *Brachyuromys*. In the latter, the height of the basisphenoid is not increased; it slopes considerably downwards from before backwards, so that the shallow pterygoid fossæ are situated slightly below the level of the inferior surface of the basisphenoid, which broadly separates them. In *Microtinae* they are situated somewhat *above* the level of the basisphenoid.

Winge, speaking of the *Bathyergini*, remarks that the strongly developed m. pterygoideus which is inserted alongside the centra of the sphenoida has transformed the presphenoid into a thin vertical plate<sup>1</sup>. I find that both the presphenoid and basisphenoid are thus transformed, at least in the genera *Bathyergus* and *Georchus*.

2. *Spalax*.—Winge places *Spalax* amongst the Dipodidæ<sup>2</sup> on account of the form of the infraorbital canal, and for having m. 1 of the same size as m. 2. He states though, that besides the complete absence of premolars, this genus is in other respects as well on a somewhat higher level than the rest of the Dipodidæ. The outer wall of the infraorbital canal is certainly not greatly developed; and in adult specimens it is besides pushed considerably forwards, whilst at the same time starting almost horizontally from the cranium. The upper maxillary radix of the zygoma, which in Muridæ usually forms the roof of the infraorbital canal, is more obliquely extended downwards in *Spalax* (not much differing from what obtains in *Zapus*), so that it helps to form the outer wall of the canal. The direction and extension of the walls, of course, shape the form of the canal itself. But with all that, the agreement with the Dipodidæ is not so considerable, and besides seems to be a secondarily acquired character in *Spalax*; and this for the following reasons:—

(1) In younger specimens of *Spalax* (B.M.), and in some adult, the outer wall of the canal is by no means pushed considerably forwards and neither is it horizontal, but more upright; as a consequence these specimens approach *Siphneus* in the form of the canal.

<sup>1</sup> 'Gnavere fra Lagoa Santa,' p. 127, and footnote 62, p. 169: "Den Del af *M. pterygoideus internus*, der voxer op paa Siderne af Kilebenskroppene, er meget stærk, naar langt frem under *Foramen opticum* og har omformet det forreste Kilebenskrop til en tynd lodret Plade." Footnote (p. 169): "De paa-gældende Muskler ere gjennemgaaede hos *Georchus capensis*; Mærkerne paa Hovedskallen ere de samme hos de andre Slægter."

<sup>2</sup> 'Gnavere fra Lagoa Santa,' pp. 109, 121, 166.

(2) In *Rhizomys*, placed amongst the Muridæ by Winge himself, the outer wall parts from the skull almost horizontally and is not only pushed forwards but upwards as well; this last Winge considers to be a secondarily acquired character<sup>1</sup>. And I think rightly; for in the closely related *Tachyoryctes* we meet with almost the normal Muridæ-type of the outer wall and the canal itself.

(3) In the powerful development of the maxillary process of the zygoma and corresponding reduction of the malar bone, *Spalax* appears to be on a higher level than the Dipodidæ; a circumstance which has not been overlooked by Winge<sup>2</sup>.

Whilst placing *Spalax* with some hesitation in the Dipodidæ, Winge does not in the least insist upon a sharp separation of *Spalax*, *Rhizomys* (and *Siphneus*), for he states expressly<sup>3</sup>: "*Spalax*, *Rhizomys*, and *Siphneus* are not widely separated animals; they take their origin from nearly related forms; there is no very great difference between a primitive Dipodide and little more or less primitive Murides."

The inevitable conclusion is, that if the *Rhizomyes* (*Rhizomys* and *Tachyoryctes*)<sup>4</sup> are to be considered as low Muridæ, and herewith I agree completely, *Spalax* has the same claims. In the comparatively powerful development of the malar bone, and in the form of the zygoma (considerable height of the anterior part), the *Rhizomyes*, *Tachyoryctes* more than *Rhizomys*, occupy an even lower rank than *Spalax*. The outer wall of the infraorbital canal in *Spalax* is scarcely less developed than in *Cricetus*.

The pattern of the molars in *Spalax*, to judge from the youngest available stages, is the same as in *Tachyoryctes* and *Brachyuromys*, whilst it agrees somewhat less with *Dipus*, with which it is compared by Winge. The relative dimensions between m. 1 and m. 2 are as in *Tachyoryctes*; m. 1 is slightly larger. Brandt assigns two roots to the molars of *Spalax*<sup>5</sup>; but the upper molars have three roots as in *Rhizomys* and *Tachyoryctes*, two outer ones and a much larger inner one. They are far from being as hypselodont as in *Tachyoryctes*, being shorter even than in *Rhizomys*. Moreover, they are somewhat atrophied, very small, and of roundish contours; the enamel-folds are rather superficial, so that the pattern becomes sooner simplified than in the two genera named. Some compensation is given by the thickness of the enamel bordering each molar. In correspondence with the much shorter molars, the maxillary bone, too, has not acquired such a great vertical extent as it has in *Rhizomys*, and still more so in *Tachyoryctes*; but the presphenoid has followed the general elevation of the middle part of the cranium; whilst remaining compact superiorly and inferiorly, its intermediate region has been transformed into a thin plate. The basisphenoid has been transformed in a similar manner, as we have seen to be likewise the case in *Rhizomys* and *Tachyoryctes*.

<sup>1</sup> 'Gnavere fra Lagoa Santa,' p. 124.

<sup>2</sup> *L. c.* p. 121.

<sup>3</sup> *L. c.* p. 167.

<sup>4</sup> For *Siphneus* see below.

<sup>5</sup> 'Craniologische Entwicklungsstufen,' p. 215: "alle besitzen zwei kurze Wurzeln, eine hintere und eine vordere."



3. *Siphneus*.—Gerrit Miller has recently expressed the opinion that it may eventually prove necessary to unite the "*Siphneinae*," i. e. *Siphneus* and *Ellobius*, with the *Microtinae*<sup>1</sup>. This corresponds fairly with Alphonse Milne-Edwards's views, who has considered the "*Siphnés*" to be "des Arvicoles anormaux."<sup>2</sup> O. Thomas maintains the subfamily for *Siphneus* alone, since according to his view its "differences, both external, cranial, and dental, are clearly sufficient to demand separate subfamily rank."<sup>3</sup>

It is to be remarked that Winge has treated the question of the relationship of *Siphneus* exhaustively many years ago. Whilst uniting *Ellobius* with the *Microtinae*, he considers *Siphneus* to be a lower type, and accordingly places it with the *Cricetinae*; its resemblance with the Voles resting solely on their having open roots to the molars, which otherwise are not different from the "*Hesperomys*-type." He points out that no Vole has such a small m. 1 inf., with not more than the usual five loops. Winge shows besides, that *Siphneus* lacks the powerful crest in the wall of the temporal fossa, which gives the characteristic feature to the Microtine skull, whereas the temporal muscles are inserted on the surface of the skull in the same manner as in the *Criceti*; and that the basioccipital region and the centrum of the basisphenoid are broader, the tympanic bones smaller, than in the Voles<sup>4</sup>. In the more simple structure of the molars he sees an indication of closer relationship with "*Cricetulus*." The shape of the outer wall of the infraorbital canal is said to be about as in the Hamsters; likewise the zygoma and the crests on the cranium, only slightly stronger; and equally the flattening and forward inclination of the occiput, the only difference being that these characters too are more strongly developed than in the Hamsters<sup>5</sup>.

It seems to me that there is little to object to Winge's view of the question; I would even go a little farther still. In his arrangement of the Muridæ<sup>6</sup>, Winge opposes his *Rhizomyini* (i. e. *Cricetodon*, *Eumys*, *Rhizomys*) to the rest of the Muridæ, m. 1 in the former being only slightly larger, in the latter considerably larger than m. 2.

As regards this character, *Siphneus* certainly belongs to the former group, with more right than *Cricetodon* and *Eumys*, which both herein are scarcely different from the *Hesperomyes*. In pattern and size the two anterior molars of *Siphneus* agree as much with each other as they do in *Spulax*, *Tachyoryctes*, and

<sup>1</sup> Gerrit S. Miller, "Genera and Subgenera of Voles and Lemmings" (North-American Fauna, No. 12, p. 8, footnote 3). Washington, 1896.

<sup>2</sup> H. Milne-Edwards et Alph. Milne-Edwards, 'Recherch. p. servir à l'Hist. nat. des Mammifères etc.,' t. i. Texte. pp. 76-79, Paris, 1868-74.

<sup>3</sup> O. Thomas, "On the Genera of Rodents" (P. Z. S. p. 1021 footnote 1). London, 1896.

<sup>4</sup> This does not hold good, however, with regard to all the genera of *Microtinae*, e. g. *Fiber* and *Ellobius*.

<sup>5</sup> H. Winge, "Om græske Pattedyr" (Videnskab. Meddel. fra d. Naturh. Foren. Kjöbenhavn for Aaret 1881, pp. 47-49. Kjöbenhavn, 1882; see also H. Winge, 'Gnavere fra Lagoa Santa,' pp. 124, 125, 126).

<sup>6</sup> 'Gnavere fra Lagoa Santa,' p. 125.

*Brachyuromys*, and even less than in some of the *Rhizomys* (especially with regard to the lower molars). In the shape of the outer wall of the infraorbital canal, *Siphneus* shows closer agreement with *Tachyoryctes* (especially with *T. splendens*) than with *Cricetus*, the lower portion of the outer wall advancing more forward. There is likewise more similarity than with *Cricetus* in the form of the canal itself, which in *Tachyoryctes* and *Siphneus* is broader in its upper part than in the first-named genus, whereas (apparently as a consequence of the broadening of the skull) in both the inferior, narrower part appears considerably shortened vertically. In this respect *Tachyoryctes* is somewhat intermediate between *Cricetus* and *Siphneus*. The malar bone of *Siphneus* is stronger than in *Cricetus*; in *S. armandi* it is as strongly developed and reaches nearer to the lachrymal than in *Tachyoryctes*. As regards the flattening and inclination of the occiput, there are different gradations in this respect in the genera under consideration (*Spalax*, *Siphneus*, *Rhizomys*, *Tachyoryctes*); one end of the series is occupied by *Spalax*, the other by *Tachyoryctes*. In the latter the inclination is scarcely more than in *Cricetus frumentarius*; in old individuals scarcely less than in young *Spalax*.

For the rest the skull of *Siphneus* is transformed to be used as a shovel and drill in a similar way as in *Spalax*.

*The Molars of Brachyuromys as compared with those of other Muridae and of Mammalia generally.*

A few introductory remarks are indispensable.

In Didelphidæ and many Insectivora there are on the outer side of the upper and on the inner side of the lower molars three very conspicuous cusps. These are considered by Winge<sup>1</sup> to be the oldest, most primitive parts of the Mammalian molar. They are the same which Osborn in upper molars has called *parastyle*, *mesostyle*, *metastyle*<sup>2</sup>; in Winge's plates<sup>3</sup> they are designated from before backwards by 1, 2, 3. The middle one is supposed to be the oldest of the three, so that according to Winge's view the protocone is something *toto cælo* different from Cope's and Osborn's protocone; this last, 6 in Winge's figures, is according to the latter author one of the latest additions to the tooth.

If we review the more primitive Ungulates and the Ancylopoda, we find equally three outer cusps in the superior molars; but it may be seen at once—and in this I think I am in agreement with Winge—that they are not homologous in the different groups.

<sup>1</sup> H. Winge, "Om Pattedyrenes Tandskifte, især med Hensyn til Tandernes Former." Vidensk. Meddel. Naturh. Foren. i. Kjöbenhavn, 1882, p. 15, pl. iii.

<sup>2</sup> See e. g. H. F. Osborn, "The Rise of the Mammalia in North America," Address, Boston, 1893, p. 35 (text-figure of *Anchitherium*). H. F. Osborn and C. Earle, "Fossil Mammals of the Puerco Beds," Ann. Mus. Nat. Hist. vol. vii. Art. i., New York, 1895, p. 44, fig. 14.

<sup>3</sup> *L. c.* pl. iii. H. Winge, "Jordfundne og nulevende Pungdyr (Marsupialia) fra Lagoa Santa, Minas Geraes, Brasilien. Med Udsigt over Pungdyrenes Slægtskab" ("E Museo Lundii"), Kjöbenhavn, 1893, pl. ii. figs. 2a, 2b, 8b, 10.

In the Anthracotherina, *e. g.* in *Ancodus*<sup>1</sup>, and in the *Ancylopoda*<sup>2</sup>, we find three widely bulging cusps in the upper molars. In *Hyracotheria*<sup>3</sup> it is easy to see that the two posterior of the three outer cusps have nothing whatever to do with the two posterior of *Ancodus* and the *Ancylopoda*; only their anterior one, which I consider as homologous with cusp 1 of Insectivora and *Didelphys*, is the homologue of the anterior cusp in *Hyracotheria*. The two posterior cusps of *Ancodus* and the *Ancylopoda* are 2 and 3; those of the *Hyracotheria* are the homologues of the two cusps more internally situated in the former, Winge's 4 and 5, Osborn's *paracone* and *metacone*: the comparison with other *Hyracotheria*<sup>4</sup>, in which something more of these "-styles" is preserved, shows this at once to be the case. The posterior outer cusp in upper molars, Winge's 3, Osborn's *metastyle*, which is so well developed in *Didelphys* and in many Insectivora<sup>5</sup>, is, when met with at all in other orders, generally the least developed of the three outer cusps, and there is sometimes a relation in its development with that of the antero-internal cusp in lower molars, Winge's 1, Osborn's *paraconid*.

The fact, pointed out by Winge, that these cusps of Insectivora and Didelphynæ have their homologues in other orders, chiefly in the older members, is of the greatest importance and a notable progress in our knowledge of the homologies of the Mammalian molar. It is a very remarkable fact, that this outermost series of cusps is enormously developed in several upper molars from the Laramie Cretaceous<sup>6</sup>. Whether we have to consider them, with Winge, as being the most primitive parts of the molar, older than the cusps situated internally from them in upper, externally in lower molars, is quite another question, in which it is not proposed to enter particularly for the present.

As regards the Rodents, Winge points out the remnants of this

<sup>1</sup> *Cf.*, *e. g.*, Zittel, 'Handbuch d. Paläontologie,' iv. p. 329, fig. 266.

<sup>2</sup> Zittel, *l. c.* p. 314, fig. 255.

<sup>3</sup> J. L. Wortmann, "Species of *Hyracotherium* and allied Perissodactyles from the Wahsatch and Wind River Beds of North America," *Am. Mus. Nat. Hist.* vol. viii., vi. 1896, p. 89, fig. 3, p. 95, fig. 4; Zittel, *l. c.* p. 277, fig. 219.

<sup>4</sup> Zittel, *l. c.* p. 243, fig. 179, p. 242, fig. 171 (*Pachynolophus siderolithicus*); Wortmann, *l. c.* p. 108, fig. 18 (*Orcokippus*).

<sup>5</sup> Winge, *l. c.* pl. iii. fig. 1 b, 2 b, 3 b.

<sup>6</sup> *Cf.* H. F. Osborn, "Fossil Mammals of the Upper Cretaceous Beds," *Am. Mus. Nat. Hist.* vol. v. Art. xvii. pl. viii., New York, 1893. Osborn calls the molars referred to "trituberculates," and expresses his belief that they lend "overwhelming proof, if any more were needed, of the unity of origin of the molar types of the higher Mammalia from a tritubercular stem instead of from a multitubercular, as Forsyth Major has suggested" (*l. c.* p. 320). For me these Laramie "*Trituberculates*," so-called, are polybunous, as well as those figured on pl. vii.; and I have only to repeat once more that "trituberculate" and "triangular" are not synonymous. Prof. Osborn assures us (*l. c.* p. 320) that these "Laramie Trituberculates" "include a variety of forms just emerging from the primitive tritubercular stage." That is precisely what has yet to be proved. But even if we were inclined to take Prof. Osborn's assertion for granted, it would have to be shown how it happens that several of these ancient forms (E, F, pl. viii.) have in their very process of "emerging" already acquired such a luxury of "-styles" and "-conules," as to constitute by themselves alone half of the molar's crown.

old row in some genera, viz., *Allomys*<sup>1</sup> and *Pseudosciurus*; the pattern of molars of the last named he considers to be the most primitive amongst known Rodentia<sup>2</sup>. He places *Pseudosciurus* in the Anomaluridæ, from which family he derives the Hystriidæ and Dipodidæ, and from the latter the Myoxidæ and Muridæ<sup>3</sup>.

I have many years ago<sup>4</sup>, and so had Hensel<sup>5</sup> before me, drawn attention to the great resemblance of the molars of *Pseudosciurus* to those of Ungulates; they were compared by me in the first line with the molars of "*Hyracotherium siderolithicum*." With regard to *Allomys* I refer to a more recent paper of mine<sup>6</sup>. Besides, I wish to draw attention to a fact, which will be more fully considered by me in another place, viz., that amongst the *Sciuropteri* we equally meet with traces of these ancient outer cusps, namely in *S. pearsoni*<sup>7</sup>, and especially in *S. xanthipes*, Milne-Edw., of which a less worn dentition than that figured by Milne-Edwards<sup>8</sup> lies before me (B.M. no. 95. 7. 5. 1).

These ancient cusps are further met with in *Aplodontia*, in whose premolar and molars the middle outer cusp in upper, and the middle inner cusp in lower molars, Winge's 2, are the most conspicuous of the three. Coues considered *Aplodontia* to be a very primitive genus, adducing for one of his reasons that the molars are of the most simple type<sup>9</sup>. There is no doubt that this genus is a very low form of Rodentia<sup>10</sup>, as shown by the skull—in spite of its highly fossorial specialization—and by the structure of the molars; but not for the reason adduced by Coues; for in an unworn condition, as figured by Schlosser<sup>11</sup>, they are shown to be of a complicated type.

We have next to face the question, what becomes of these ancient outer cusps in the upper molars of Mammals generally? Years ago I tried to show that the vertical ridges on the outer side of the molars of modern Ungulates are not the unimportant parts which they are generally held to be<sup>12</sup>; and Winge has since identified them as the homologues of the outer series (1, 2, 3) of Insectivora and Polyprotodontia<sup>13</sup>. In proportion as the next following inner cusps, 4 and 5, increase in size and at the same time apparently move outwards, the outer cusps decrease and either become fused with 4 and 5, or persist between them in the

<sup>1</sup> 'Gnavere fra Lagoa Santa, etc.,' p. 114.

<sup>2</sup> *Ib.* p. 116. <sup>3</sup> *Ib.* p. 110 etc.

<sup>4</sup> Palæontographica, vol. xxii. 1873, p. 76.

<sup>5</sup> Zeitschr. d. deutsch. geol. Ges. viii. 1856, p. 664.

<sup>6</sup> "On some Miocene Squirrels etc.," P. Z. S. 1893, pp. 192, 193.

<sup>7</sup> *Ib.* pl. viii. fig. 20.

<sup>8</sup> 'Rech. p. servir à l'Hist. nat. des Mammifères,' Paris, 1868-74, p. 171, pl. 15 A. fig. 3.

<sup>9</sup> E. Coues and J. A. Allen, "Monographs of North-American Rodentia," Report Un. St. Geol. Survey of the Territories. Washington, 1877, p. 555.

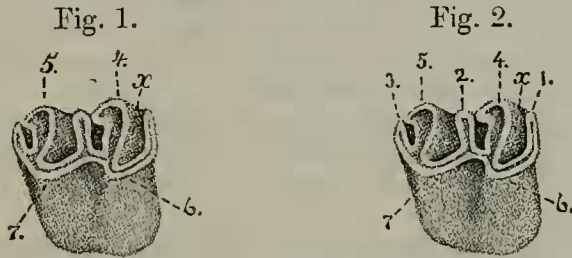
<sup>10</sup> See Winge, 'Gnavere fra Lagoa Santa,' pp. 108, 110, 115.

<sup>11</sup> M. Schlosser, "Die Nager des europäischen Tertiärs," Palæontographica, xxxi. 1884, p. 106 (124).

<sup>12</sup> "Nagerüberreste aus Bohnerzen Süddeutschlands und der Schweiz," Palæontographica, xxii., 1873.

<sup>13</sup> "Om Pattedyrenes Tandskifte etc.," *l.c.* pl. iii.

same longitudinal row. Winge has summed up in a few words his view of the fate of these outer cusps<sup>1</sup>. But in the figures of upper Rodent molars he ignores what I consider to be their homologues. For a clearer understanding of what is to follow, I append two sketches of the same upper molar from Winge's plates, the first with the numbering given by this author, the second with the numbering according to the manner in which I grasp the homologies. The tooth figured is one of the *Hesperomyinae* with more complicated molars, being a copy of fig. 12 a, pl. iii. of Winge's paper<sup>2</sup>, representing the second right upper molar of "*Nectomys squamipes*" (text-figs. 1 and 2). Winge assigns the homologies



Second right upper molar of *Nectomys squamipes*, after Winge.

thus:  $\frac{5\ 4}{7\ 6}$ , taking into consideration only what in these teeth appear to be the principal cusps; whereas I would write them as follows:  $\frac{3\ 5\ 2\ 4\ 1}{7\ 6}$ , taking into consideration as well those which in these teeth appear to be merely secondary cusps<sup>3</sup>.

Now as to *Brachyuromys*. Here we have as principal feature of the molars three transverse and somewhat oblique rows. In *Brachyuromys ramirohitra* the separation of the three rows, their obliquity and their lophodontism are more pronounced than in *B. betsileoensis*, whose unworn teeth show a half-tuberculate conformation and are therefore more fit for the understanding of the homologies.

*M. 2 sup.* (Plate XXXIX. figs. 1 a, 2 a, 3 a, 7 a, 8 a).—The anterior transverse row apparently is composed of the outer cusp 1 and the inner cusp 6. The second one is a compound, on the outer side, of '4' anteriorly and '2' posteriorly, which in very early stages become fused with each other and with the inner cusp 7. The most prominent outer and inner cusps,

<sup>1</sup> "Kronen bliver ved sin Væxt saa bred, at Underkjæbe tænderne ere for smalle til endnu at røre ved dens ydre Rand, naar Munden lukkes; derfor vantrives de tre oprindelige yderste Spidser og indskrænkes til fremspringende Hjørner eller Lister, smelte sammen med de nærmeste indre Spidser eller forsvinde helt" (Om Pattedyrenes Tandskifte, etc., l. c. pp. 17, 18; see also footnote 4 on p. 41).

<sup>2</sup> 'Gnavere fra Lagoa Santa, etc.'

<sup>3</sup> On comparison of the lower molars figured in Plates XXXIX. and XL. of the present paper with those on pl. iii. of Winge's "Om Pattedyrenes Tandskifte, etc.," it will be seen that my mode of numbering the cusps to indicate their homologies disagrees with the one adopted by Winge; but I cannot in this paper enter into a discussion of my mode of viewing the homologies of lower molars.

viz. 4 and 6, 5 and 7, are opposed to each other in a similar way as in *Hesperomys*; the oblique position of the rows is brought about by the different connections. The third, posterior, row, which remains essentially limited to the outer part of the posterior margin, shows on unworn teeth of both species, more distinctly in *B. betsileoensis*, its composition of two parts: an anterior somewhat stronger cusp, 5, and a posterior smaller one, 3; exactly as in the less reduced teeth of *Hesperomys*<sup>1</sup>.

The lower molars agree with the upper ones, if we take into account that they are, of course, reversed. The anterior transverse row, restricted to the inner part, consists, as seen in unworn teeth of *Brachyuromys betsileoensis* (Plate XXXIX. fig. 7*b*), of Winge's 1 and 4. The middle row consists internally of 2 and 5, which very soon become fused with the outer cusp 6. The posterior ridge is composed of 3 and 7.

To sum up. The five transverse ridges of *Trechomys*, e. g.<sup>2</sup>, or of the Dipodide *Zapus*, are in *Brachyuromys* reduced to three, by the atrophy of 2 and 3 and their fusion with 4 and 5.

*Comparison of the Molars of the "Rhizomyes" (Tachyoryctes, Rhizomys) with those of Brachyuromys.*

It has been formerly stated that the molars of *Brachyuromys ramirohitra* are almost identical with those of the African *Tachyoryctes*<sup>3</sup>. There is, however, a greater difference in vertical extension between the molars of the two genera than appears from my former statement: those of *B. ramirohitra* are semi-hypsodont, whereas the very hypselodont molars of *Tachyoryctes* are on their way to become rootless. In *Rhizomys* the molars are less hypselodont than those of *Tachyoryctes* and somewhat more complicated than in both *Tachyoryctes* and *Brachyuromys*.

This is particularly apparent in the molars of the upper jaw. While in the latter genus we have seen the upper molars to be composed essentially of three outer cusps (3+5; 2+4; 1), separated by two external folds, there are four cusps in *Rhizomys* and accordingly three folds, which later on become three enamel islets. In *Rh. badius* the teeth, although as complicated in an unworn condition as those of the other species, become when worn more similar to the unworn teeth of *Tachyoryctes* and *Brachyuromys*, a fusion taking place in the anterior part of the crown. Moreover, the gradual disappearance of the islets from the crown proceeds at a quicker rate than in the other species of *Rhizomys*.

In *Tachyoryctes*, m. 1 sup. of young specimens has a similar structure to that of all three molars of *Rhizomys*. But this complication too disappears very soon, so that somewhat worn anterior molars of

<sup>1</sup> R. Hensel, "Beiträge z. Kennt. Säugeth. Süd-Brasiliens," Phys. Abh. k. Akad. d. Wiss. Berlin, 1873, pl. i. figs. 24*a*, 25*a*; pl. ii. figs. 26*a*, 28*a*; pl. iii. fig. 30*a*.—Winge, 'Gnavere fra Lagoa Santa, etc.,' pl. iii. figs. 1*a*, 10*a*, 12*a*.—It is also apparent in several Muridae, e. g. *Uromys*, *Conilurus* (young), *Chiruromys*.

<sup>2</sup> Winge, 'Gnavere fra Lagoa Santa,' p. 116.

<sup>3</sup> P. Z. S. 1896, p. 979.

the former are perfectly similar to the following tooth and to those of *B. ramirohitra*, even in the oblique direction of the transverse ridges: whereas in *Rhizomys* these are placed at right angles to the long axis of the skull. As in *B. ramirohitra*, m. 3 sup. of *Tachyoryctes* is longer than the two anterior, this being a consequence of a fuller development of its posterior portion; that is, 3 remains longer independent from 5.

The different proportional size between the molars of *Tachyoryctes* and those of *Rhizomys* is apparently to a great extent due to the influence exercised by the incisors. In old specimens of *Tachyoryctes* (Plate XXXIX. fig. 6 a) the upper molars increase in size from before backwards. The upper incisors in this genus form a smaller segment of a circle than in *Rhizomys*, so that their posterior end interferes with the development of m. 1. In the latter genus the segment is a larger one; as a consequence, the first molar is partly or totally (according to the different species) withdrawn from the influence exercised by the incisor, which interferes with the posterior molars.

In *Rh. badius* the hinder end of the incisor reaches farther backwards than in any other species: m. 1, which is from the beginning the largest of the three (Plate XL. figs. 1 a, 2 a), remains such to an advanced stage of wear (Plate XL. fig. 3 a); the two posterior molars soon diminish in size. This decrease in size, from m. 1 to m. 3, is more intensified with age.—In *Rh. sumatrensis*, the incisor does not seem to affect the molars, their proportional size remaining the same in youth and advanced age (Plate XL. figs. 5 a, 6 a); m. 3 sup. is very small from the beginning.—In *Rh. pruinus* and *Rh. sinensis* (Plate XL. fig. 7 a) the incisor forms a smaller segment of a circle than in *sumatrensis*, and a much smaller one than in *badius*. I have not all the stages of wear of *Rh. sinensis*, but there seems to be no essential difference from *Rh. pruinus*. In this latter the unworn m. 1 sup. is considerably elongate (Plate XL. fig. 4 a); very soon it becomes reduced to the size of m. 2, and in very old dentitions it is even smaller than the latter.

To recapitulate the foregoing with regard to the two extremes, *Rhizomys badius* and *Tachyoryctes*. In both, m. 1 sup. is, before wear, slightly larger and especially longer than m. 2. In old specimens of *Rh. badius* both teeth, unaffected by the incisor, maintain their relative proportions, whereas both become considerably reduced in *Tachyoryctes*. The latter's m. 1, which is the most interfered with by the incisor, is eventually reduced to the size of m. 2, and in old individuals becomes even somewhat smaller; m. 1 becomes equally much reduced in size. In *Tachyoryctes* the greater vertical extension of the molars is a further reason for their being very soon interfered with by the incisor. M. 3, which from the beginning is somewhat atrophied in *Rh. badius*, becomes more so with advance of wear; whilst in *Tachyoryctes*, where the posterior part of m. 3 is on the contrary somewhat produced, as compared with its anterior molars, and with m. 3 of *Rh. badius*, this tooth maintains its proportions even in old individuals.

As regards the pattern of the *Rhizomys* molars, it results from a comparison with those of *Brachyuromys* and *Tachyoryctes*, that in *Rhizomys* cusp 2 maintains its independence, whereas in the others, as shown by *B. betsileoensis*, this cusp is not even in young specimens strongly developed, and becomes soon fused with 4. The homologies of the four outer cusps of *Rhizomys* are therefore to be expressed by the following figures:—1; 4; 2; 5+3 (see Pl. XL. figs. 1 a–7 a).

Of the lower molars of *Rhizomys* (Pl. XL. figs. 1 b–8 b) m. 1 is constantly longer and more complicated than either of the two posterior molars, which last agree almost absolutely with each other in size and pattern. Internally some of the species show, when young, four cusps, the two anterior of which are not strongly separated, so that very soon the only remainder of the original separation is a small enamel islet, which too tends to disappear. In *Rh. badius*, 1 and 4 appear already fused from the beginning, *i. e.* in the youngest available stages. The homologies of the four cusps, as compared with *Brachyuromys*, are therefore as follows: 1; 4 (or 1+4); 2+5; 3. I feel justified in considering the third cusp to be, as in *Brachyuromys*, a compound of two (2+5), from what is visible in unworn posterior molars as compared with m. 1 (Pl. XL. fig. 1 b, 2 b, 4 b, 5 b, 6 b). M. 1 is besides distinguished by a *surplus* on the antero-internal side: not only is cusp 1 separated from 4, but, like m. 1 of *Rh. betsileoensis*, there is an antero-external cusp in addition to what obtains in m. 2 and m. 3.

The molars of *Rhizomys* therefore, besides being less hypselodont than those of *Tachyoryctes*, are also more complicated than the molars both of the latter genus and of *Brachyuromys*, and thus approach more to the brachyodont amongst Malagasy Rodents; and further on to some members (*Trechomys*, *Theridomys*) of a more primitive group, Winge's *Anomaluridae*. The molars of *Tachyoryctes* and *Brachyuromys*, on their side, show a remarkable likeness in pattern to some other members of the same group, *viz.* *Protechimys*<sup>1</sup>, *Archæomys*. The molars of the former genus, which are much more brachyodont than those of the latter, arrive at the more simplified pattern of *Archæomys*, only in a somewhat advanced stage of wear. In comparing the molars of these two genera with each other and with *Brachyuromys* and the *Rhizomyes*, it becomes evident, beyond doubt, that the simplified pattern of the molars is the outcome of a complicated one. This is further confirmed by the little we know of a Pliocene *Rhizomys*, *viz.* :—

*Rhizomys sivalensis*, Lydekker<sup>2</sup>, less specialized still than the existing *Rhizomys*.—I have reproduced the enlarged molars (Pl. XL. fig. 9 b) from a right mandibular ramus in the British Museum, No. 15925, mentioned in the Catalogue. Lydekker says of the

<sup>1</sup> Cf. "*Theridomys blainvillei*, Gerv.," in Gervais, Zool. et Pal. franç. pl. 47. fig. 17.—M. Schlosser, "Die Nager des europäischen Tertiärs," Palæontographica. xxxi. 1884, pp. 63 (45)—68 (50), pl. ix. (v).

<sup>2</sup> Records Geol. Surv. India, xi. 1878, pp. 100, 101, xii. 1879, p. 41; id. Pal. Ind. x., iii. 1884, p. 107–108; id. Catalogue of the Fossil Mammalia in the British Museum (Natural History), i. London, 1885, p. 233.



*Rh. sivalensis*, speaking of specimens in the Indian Museum, Calcutta:—"The relatively wider molars and the larger size of the incisors of the existing forms as compared with those of the fossil seem to indicate that the specialization has tended to the production of these characters."<sup>1</sup> In a former paper<sup>2</sup> it had been stated that "the fossil molars are in one specimen slightly smaller, and in the other slightly larger than those of the recent species" (i. e. *Rh. sumatrensis*).

In the mandibulæ preserved in the British Museum, the molars are wider and longer than those of the largest living species (*Rh. sumatrensis*), although the mandibula is shorter and lower. The elements constituting each of the molars in the recent forms appear to be more crowded together antero-posteriorly than in the fossil. In this last the molars are more complicated and remain so even in a worn condition, cusp 1 not becoming fused with 4, an occurrence which we meet with only in very young stages of some of the species of living *Rhizomys*. Besides, as has been already pointed out by Lydekker, in the fossil molars the external fold has a greater depth than in recent species. To sum up. The molars of *Rh. sivalensis* preserve the main characters of the molars of young specimens in later age, whilst in all the recent species the molars are very soon simplified, in some a little earlier, in others a little later.

*Comparison of the Molars of the Hesperomyinæ with those of  
Brachyuromys and Nesomys.*

Amongst American Muridæ the simplification of the pattern of molars has been attained in two ways: (1) by a more or less complete suppression of 1, 2, 3, accompanied by a predominance of the four cusps 4, 5, 6, 7, notably the two former; so that the crown of m. 2 remains essentially composed of four cusps; (2) by a more or less complete suppression of 2 and 3, whilst 4, 5, 6, 7 are equally somewhat reduced in dimensions, whereas 1 is rather increased; at any rate it has obtained quite or almost the dimensions of 4 and 5. Of both molars Hensel and Winge have figured examples. To the latter belong such genera as *Sigmodon (hispidus)*, *Holochilus (vulpinus)*, and the *Neotomince*. Whilst in the former there exists a notable difference in form and size between m. 1 and m. 2, as in the *Hesperomyinæ* with more complicated molars<sup>3</sup>, in the latter m. 1 tends to become more similar to m. 2.

Of the first type, viz. brachyodont, bunodont molars, with essentially only four tubercles, I have found no parallel amongst living Malagasy Rodents; but I discovered in the lower deposits of the "Children's Cave," near Sirabè (Central Madagascar), some jaws belonging to this type; these will be dealt with on a future occasion. To the second type belongs, amongst Malagasy Rodents, *Brachyuromys*; and from other parts of the Old World,

<sup>1</sup> Pal. Ind. l. c. p. 108.

<sup>2</sup> Rec. Geol. Surv. Ind. xi. 1878, p. 101.

<sup>3</sup> Of course, as was shown so long ago as 1873 by Hensel, there are all possible transitions to be found between the simple and the more complicated molars.

*Tachyoryctes* (in a lesser degree *Rhizomys*), *Spalax*, and *Siphneus*. In the great agreement between m. 1 and m. 2, there is a decided approach of *Neotominae* to all these Old World forms; there are species of *Neotoma*<sup>1</sup> in which scarcely any difference between m. 1 and m. 2 can be found. Of course this character, common to the two groups, may be partly the result of both having hypselodont molars.

One important character in the skull shows that the Old World Muridæ under consideration are on a lower level than the *Neotominae*. With the exception of *Spalax* they all have the jugal greatly developed and approaching the lachrymal, whereas in *Neotominae* the jugal is extremely reduced.

Of the *Hesperomyinae* with a more complicated pattern there are likewise parallels in Madagascar, viz. *Hallomys*<sup>2</sup> and *Nesomys*. These two genera will be more fully described on a future occasion; but I append here a short characteristic of the dentition of the latter. I consider these complicated molars to be a more primitive condition than the simpler form, for reasons which will be fully discussed further on.

Fig. 3.

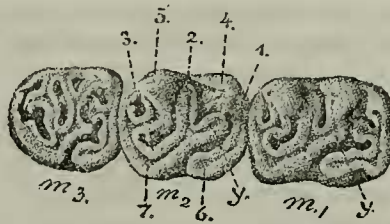
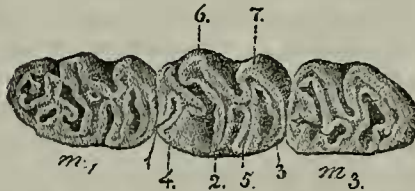
Right upper molars of *Nesomys rufus*.

Fig. 4.

Right lower molars of *Nesomys rufus*.

The molars of *Nesomys* figured in the text (text-figs. 3 & 4) represent the youngest stage I have been able to procure. In this stage of wear the teeth are half-tuberculate, the outer tubercles in upper, and the inner tubercles in lower molars being more cuspidate than the inner tubercles of upper and the outer ones of lower molars. In this as well as in other respects they approach nearer to such forms amongst *Hesperomyinae* as "*Hesperomys squamipes*,"<sup>3</sup>

<sup>1</sup> C. Hart Merriam, "A new Subfamily of Murine Rodents—the *Neotominae*," Proc. Acad. Nat. Sci. Philadelphia, 1894, p. 240, fig. 5 a, b.

<sup>2</sup> Since the above was written, I have seen in Leyden the type specimens of *Hallomys audeberti*, Jent., which proves to be a species of *Nesomys*.

<sup>3</sup> Hensel, l. c. pl. i. fig. 24, pl. ii. fig. 14.

"*Nectomys squamipes*,"<sup>1</sup> "*Hesperomys dorsalis*,"<sup>2</sup> "*Hesperomys tumidus*."<sup>3</sup> As in the *Hesperomyine* just mentioned, cusps 2 and 3 are well developed in *Nesomys*, and had younger stages been at hand, these cusps would have probably shown to be as independent from 4 and 5 as they are in Winge's fig. 12 *a*.

A feature common to the upper and lower molars of *Nesomys*, as compared with *Hesperomyine*, is a reduction in size of the cusps 4 and 5, and a corresponding increase in size and greater independence of the adjoining parts, of what I consider to be the homologue of the "intermediate" cusps of *Sciuroides*, *Pseudosciurus*, and of many, especially the older Placentals. Of this more will be said below, when m. 1 sup. of *Nesomys* will be discussed as compared with the same tooth of *Murine*.

Another distinguishing feature of the upper molars m. 1 and m. 2 of *Nesomys*—in which, by the way, they approach somewhat to the *Murine*, as well as in the greater development of the intermediate cusps—as compared with the *Hesperomyine*, is the lesser degree of symmetry between the anterior and the posterior part of the molars (see m. 1). In the *Hesperomyine* the enamel-fold, penetrating from the inner side (in upper molars), is separated from the anterior valley (*x* in text-figs. 1 & 2, p. 707) by a ridge—apparently the homologue of the intermediate cusp—connecting the outer cusp 4 with the inner cusp 6. In *Nesomys* the interspace formed by the enamel-fold mentioned is confluent with the anterior valley, thus separating cusp 6 from connection with the outer cusp 4, or rather with the intervening intermediate cusp (*y*, fig. 3)—a state of things which is only arrived at in much worn molars of *Nesomys*; whilst in this respect *Brachyuromys betsileoensis* agrees with the *Hesperomyine*.

Obviously, the formation of transverse ridges in molars by means of a fusion of the outer with the inner cusps (*lophodonty*) is brought about with the participation of the "intermediate" cusps, which, e. g. in *Pseudosciurus* and *Sciuroides* amongst Rodents, are as yet independent. This holds good with regard both to upper and lower molars.<sup>4</sup> These "intermediate" or "secondary" cusps, Osborn's "*protoconule*" and "*metaconule*," are generally considered to be of secondary importance, viz. later additions to the crown, because as a rule they are inferior in size to the outer and inner cusps. When this is *not* the case, they are liable not to be recognized, and such appears to have been the case with regard to the *Murine*, amongst others. Winge derives the Murine molar from the *Hesperomyine* type, by supposing that in the former the outer cusps (of upper molars) have increased in size as compared with the latter, and that by so doing they have pushed the inner

<sup>1</sup> Winge, 'Gnavere Lagoa Santa,' pl. iii. fig. 12 *a*.

<sup>2</sup> Hensel, *l. c.* pl. ii. figs. 16, 26.

<sup>3</sup> Hensel, *l. c.* pl. iii. figs. 20, 30.

<sup>4</sup> Besides, these intermediate cusps connect the two principal transverse ridges in the molars of *Brachyuromys betsileoensis* (not so in *B. ramirohitra*), as a result of which connection we obtain the interspace (fold) on the inner side of upper, and on the outer side of lower molars, a widespread feature in Mammalian molars.

cusps forwards<sup>1</sup>. The small cusps outside from the large "outer" cusps he supposes to be a new addition in *Murinae*<sup>2</sup>. Now, it is possible to show with the help of the *Nesomyinae* (1) that these supposed new additions of *Murinae* are the homologues of the outer cusps 4 and 5 of *Hesperomyinae* and *Nesomyinae*, which in *Murinae* atrophy to a certain extent as compared with the two former groups. And (2) that those cusps which in *Murinae* Winge considers to be 4 and 5 are in reality the intermediate cusps, which in this subfamily have acquired a considerable size<sup>3</sup>.

As regards the anterior upper molar (m. 1) in *Murinae*, the anterior side of this tooth is tripartite, whereas it is bipartite in *Hesperomyinae*, which last present three *internal* cusps against two in the former subfamily<sup>4</sup>. The clue for an understanding of the homologies is afforded by some of the *Nesomyinae*, by young *Brachyuromys betsileoensis* (Pl. XXXIX. fig. 7 a), and more than all by *Nesomys* (text-figure 3). The comparison with *Nesomys* shows that the middle part of the tripartite anterior side of the Murine m. 1 is an intermediate cusp strongly developed; the outer part is cusp 1, more developed than in m. 2; the internal

<sup>1</sup> Vidensk. Meddel. fra d. Naturh. Foren. i Kjøbenhavn for Aaret 1881, Kjøbenhavn, 1882, p. 27.

<sup>2</sup> *L. c.* p. 27: "idet hver af dem" (*i. e.* ydre Knolde), "paa sin Yderside af-sætter en lille Knold, der dog ikke er skilt fra Moderknolden."

<sup>3</sup> Some years ago Prof. Osborn arrived at the conclusion that these median cusps in the upper molars of *Mus* are homologous with the "intermediate" cusps in other Placentals (H. F. Osborn, "The Rise of the Mammalia in North America," *l. c.* p. 19). He considers this to be a victorious argument against my own views, being, according to what he states (*l. c.* p. 18), an "evidence that the multitubercular molar instead of being primitive was derived from the tritubercular"; and farther on (p. 19), that "the molars of the mouse (*Mus*), and of certain kangaroo-rats (*Dipodomys* and *Perognathus*), illustrate beautifully the recent stages between trituberculy and multituberculy, showing that the intermediate tubercles of *Mus* (also common in other Placentals) give rise to the intermediate or third multituberculate row." However, in such of the Muridæ in which these "intermediate" cusps are somewhat less developed (e. g. *Nesomys*), or more or less suppressed (e. g. several *Hesperomyinae*, *Cricetus*, *Mystromys*), we do not for that reason find a nearer approach to tritubercular forms.

I am quite prepared to concede to Prof. Osborn that some of the features common to the molars of *Allotheria* and of *Murinae* may have been independently acquired in each. One might even suggest that the whole of the outer series of cusps in the upper molars of *Allotheria* are the homologues of the outer series 1, 2, 3 of Winge, and, as a consequence, that the second range in the *Allotheria* corresponds to 4, 5 of Winge (paracone and metacone of Osborn); in that case the internal range of the former would be the homologue of the intermediate cusps of more modern Mammals. It would further follow that Cope's and Osborn's protocone (Winge's 6), absent in the *Allotheria*, is in reality a later addition, as has been suggested by Winge; so would also be the postero-internal cusp (Winge's 7), in which last assumption Winge agrees with Cope, Osborn, etc. With the materials at present available, such a supposition could be neither proved nor disproved for the moment.

More to the point is, that the "intermediate" cusps of *Mus* are "also common in other Placentals," and especially in (geologically speaking) older forms; and that they are present not only in the "Laramie Multituberculates," but as well in several of those molars which have been comprised by Osborn under the denomination of "Laramie Trituberculates." (*Cf.* pl. viii. of "Fossil Mammals of the Upper Cretaceous Beds," *l. s. c.*)

<sup>4</sup> In several *Murinae* there is an additional small postero-internal cusp.

part is the antero-internal cusp 6, which, together with 7, appears always shifted forwards in *Murinae*, as was assumed by Winge<sup>1</sup>. In *Hesperomyinae* cusp 6 stands opposite the outer cusp 4; it is the median of the three internal cusps of m.1; the anterior one is the homologue of the intermediate cusp, above mentioned, of *Murinae*, which in *Hesperomyinae* occupies a more internal position. In *Nesomys* (text-fig. 3) this intermediate cusp occupies the same position as in *Murinae*, but it is much less developed than either in *Murinae* or in *Hesperomyinae*<sup>2</sup>. Owing to the smaller size of this cusp and to its position on the anterior side of the tooth, the formation of an anterior fold, *i. e.* "interspace," between this intermediate cusp anteriorly and cusp 6 posteriorly, which we have in *Hesperomyinae*, is not arrived at in *Nesomyinae*. The antero-internal cusp, 6, occupies in the latter about the same position as in the former; it is much less shifted forwards than in *Murinae*.

*Lower Molars of Nesomys.*—With regard to the lower molars in *Hesperomyinae* and *Nesomys*, there can be no doubt as to which are the two principal internal cusps. The posterior internal cusp, 3, is sometimes rather strongly developed in *Hesperomyinae*, just as in *Brachyuromys*; in other members of the group it is reduced as compared with 4 and 5, just as in *Nesomys*. In the *Hesperomyinae* the median crest, corresponding to 2, either remains rather independent, reaching the inner side, but still with the tendency to cling to the antero-internal cusp; or it is more or less intimately connected with the postero-internal cusp, 5. In the latter case we find an enamel islet as remainder of the original separation<sup>3</sup>. In *Nesomys* the median crest becomes fused, near the inner side, with the posterior part of the antero-internal cusp, 4; a configuration to which there is an approach in those *Hesperomyinae*, "*H. ratticeps*,"<sup>4</sup> "*H. longicaudatus*,"<sup>5</sup> "*H. nasutus*,"<sup>6</sup> "*H. subterraneus*,"<sup>7</sup> in which the usually independent crest leans against the antero-internal cusp.

In both *Hesperomyinae* and *Nesomys* the principal outer cusps, 6 and 7, are internally connected by a small longitudinal crest, from which the median transverse crest, 2, starts inwards at right angles. In *Brachyuromys betsileoensis* the aforesaid small longitudinal crest is likewise present, which explains the formation in this species of two creeks, an outer and an inner one, corresponding to the transverse valley in *B. ramirohitra*. In unworn teeth of *Br. betsileoensis* the median transverse ridge, 2, starting at right angles from the longitudinal crest, is equally to be seen; it

<sup>1</sup> Considering the backward inclination of the intermediate and external cusps of *Murinae*, whilst the inner cusps remain upright, it might be questioned whether the latter have shifted their place forwards, or not rather the former backwards.

<sup>2</sup> This is one of the reasons for the great similarity between m.1 and m.2 in this as well as in the other *Murinae*, as compared to what we find in the two subfamilies just mentioned.

<sup>3</sup> See the figures in Hensel, *l. c.*

<sup>4</sup> Hensel, *l. c.* pl. i. fig. 25 *b.*

<sup>6</sup> *Ib.* pl. iii. fig. 29 *b.*

<sup>5</sup> *Ib.* pl. ii. fig. 28 *b.*

<sup>7</sup> *Ib.* pl. iii. fig. 31 *b.*

connects itself, as often in *Hesperomyinae*, with the postero-internal cusp 5, with which it becomes fused at an early date (in another Malagasy genus, *Gymnuromys*, it remains independent).

Nor is the antero-internal cusp, 1+4, simple, although it is undivided in *Brachyuromys*. In the *Hesperomyinae* it presents itself frequently as a simple cusp, but in several forms, "*H. ratticeps*,"<sup>1</sup> "*H. longicaudatus*,"<sup>2</sup> "*H. tumidus*,"<sup>3</sup> it appears as composed of two parts separated by an enamel islet—an anterior smaller cusp (Winge's 1, Osborn's *paraconid*), and a posterior larger cusp (the antero-internal cusp, 4). In *Nesomys* the original compound structure of this cusp (1+4) is likewise shown, in moderately worn molars, by an enamel islet; and in very young *B. betsileoensis* it is foreshadowed by a slight depression of the enamel.

From this comparison of the lower molars of *Nesomys* with those of *Brachyuromys betsileoensis* and *Hesperomyinae*, it results that the molars of the former approach closer to certain forms of *Hesperomyinae* in the conformation of their pattern, the latter to others. The internal enamel-folds remain for a longer time open on the inner side in the teeth of *Brachyuromys* and several *Hesperomyinae* than in *Nesomys*. In the relative positions of outer and inner cusps *Brachyuromys* differs from some other *Hesperomyinae*. In both *B. betsileoensis* and *B. ramirohitra* the postero-internal cusp, 5, stands directly opposite the interspace (inlet) dividing the two outer cusps (6 and 7), so that it comes to alternate with the latter, as in "*H. vulpinus*,"<sup>4</sup> "*H. squamipes*"<sup>5</sup>; in these same *Hesperomyinae* and in *Brachyuromys* 3 is more developed, whilst 2 is atrophied. In other *Hesperomyinae* the principal outer and inner cusps are almost opposite each other, as in *Nesomys*. *Brachyuromys* agrees more with "*H. vulpinus*"<sup>6</sup> and "*H. arenicola*?"<sup>7</sup> (the former is somewhat hypselodont; the fig. of the latter presents a much worn molar); *Nesomys* with "*H. ratticeps*,"<sup>8</sup> "*H. longicaudatus*,"<sup>9</sup> "*H. subterraneus*"<sup>10</sup>. The form of "*H. squamipes*"<sup>11</sup> agrees with both of them.

As was pointed out above, a still more advanced atrophy of 1, 2, and 3 leads us to such simple forms amongst Muridæ as *Cricetus*, *Mystromys*, "*Hesperomys expulsus*,"<sup>12</sup> "*Habrothrix lasiurus*,"<sup>13</sup> "*Hesp. nasutus*,"<sup>14</sup> in which the pattern of the crown shows essentially only four cusps. Winge is doubtful whether the presence or the absence of the "transverse ridge" between the outer cusps, 4, 5, in upper, and the inner cusps in lower molars is the primitive condition in Muridæ; adding, "its presence in *Sminthus*, *Scirotetes*, and several other low Rodents leads to the assumption that this condition is the primitive one in Muridæ; whereas the absence of this 'transverse ridge' in the lowest

<sup>1</sup> Hensel, *l. c.* pl. i. fig. 25 b.    <sup>2</sup> *Ib.* pl. ii. fig. 28 b.    <sup>3</sup> *Ib.* pl. iii. fig. 30 b.

<sup>4</sup> Hensel, *l. c.* pl. i. fig. 23 b.    <sup>5</sup> *Ib.* pl. i. fig. 24 b.    <sup>6</sup> *Ib.* pl. i. fig. 23 b.

<sup>7</sup> *Ib.* pl. ii. fig. 27 b.    <sup>8</sup> *Ib.* pl. i. fig. 25 b.    <sup>9</sup> *Ib.* pl. ii. fig. 28 b.

<sup>10</sup> *Ib.* pl. iii. fig. 31 b.    <sup>11</sup> *Ib.* pl. i. fig. 24 b.

<sup>12</sup> Winge, 'Gnavere fra Lagoa Santa,' pl. ii. fig. 4 a.

<sup>13</sup> *Ib.* pl. ii. fig. 11 a.

<sup>14</sup> Hensel, 'Beitr. Kenntn. d. Säugeth. Süd-Bras.' pl. iii. figs. 19, 29.

known of Muridæ, as *Cricetodon* and *Cricetus*, would point to the opposite assumption" <sup>1</sup>.

These two genera are considered by Winge to be amongst the lowest of Muridæ, on account of the greater agreement in size of their m.1 and m.2; m.1 being more elongate in the *Murinae* <sup>2</sup>. To these views of Winge I have to object:—(1) The molars of some of the species of *Cricetodon* show the transverse ridge in question. Winge refers <sup>3</sup> to the figures of *Cricetodon* given by Gervais <sup>4</sup>, who figured worn teeth. With regard to the Tertiary Muridæ comprised under this generic denomination, the case stands thus:—In the older forms, e. g. *Cricetodon cadurecense*, Schloss. <sup>5</sup>, from the Quercy, not only the middle transverse ridge, ending in 2, but also 1 and 3 are present, as they are likewise present in *Eumys* <sup>6</sup> (which does not seem to differ much from *Cricetodon*, both being very similar to the less simple molars of many *Hesperomyinæ*). Besides, we find in *Cricetodon cadurecense* a primitive feature of m. 1 which is almost identical with m. 2. In the more recent species of *Cricetodon*, from the Middle Miocene of Steinheim and La Grive Saint-Alban, I observe a greater approach to *Cricetus*; m. 1 is larger and more complicated as compared with m. 2, and the accessory crests of all the molars tend to disappear.

(2) In the Malagasy Muridæ the difference in size between m.1 and m.2 is even less, and their agreement in form greater than in *Cricetus*, *Cricetodon*, and the *Hesperomyinæ*, which is one of my reasons for regarding them as more primitive Muridæ than the above-named. And still we have found 1, 2, and 3 to be present in molars of young *Brachyuromys betsileoensis*. In other Malagasy Muridæ, to be described on a future occasion (*Nesomys*, *Gymnuromys*, *Brachytarsonmys*), they are still more evident, and not in the least limited to young stages <sup>7</sup>.

(3) In the Tertiary such simple forms of molars as exhibited by *Mystromys*, *Cricetus*, "*Hesper. expulsus*," and "*Habrothrix lasiurus*" are not known. The latter two, apart from the pattern of their molars, agree in all the rest with the other *Hesperomyinæ* (having more complicated molars) than with *Cricetus*. The latter genus is apparently derived from some such form as *Cricetodon* by a greater reduction of its molars, just as the *Hesperomyinæ*, with simpler constructed molars, appear to be derived from those with more complicated teeth. With reference to its teeth I have therefore recently called *Cricetus* a terminal form amongst Muridæ <sup>8</sup>.

Winge has, in this conjunction, urged the similarity of the m.2 of *Cricetus* with other Mammalia <sup>9</sup>. I know of no greater agree-

<sup>1</sup> 'Gnavere fra Lagoa Santa,' p. 11; and footnote 6, p. 151.

<sup>2</sup> "Om græske Pattedyr," Meddel. Naturh. Foren. i. Kjöbenhavn, 1881; 'Gnavere fra Lagoa Santa,' pp. 123, 124.

<sup>3</sup> "Om græske Pattedyr," *l. c.* p. 22.

<sup>4</sup> Zool. Pal. franç. pl. 46. fig. 3.

<sup>5</sup> *L. c.* pl. xii. (viii.) figs. 28, 35.

<sup>6</sup> Leidy.

<sup>7</sup> In the same way the Dipodine *Zapus*, in which m.1 and m.2 are of absolutely the same conformation and size, shows likewise 1, 2, and 3 well developed.

<sup>8</sup> P. Z. S. London, 1896, p. 980.

<sup>9</sup> Meddel. Naturh. Foren. 1881, p. 26; 'Gnavere fra Lagoa Santa,' p. 11.

ment than with the molars of Cercopithecidae, which Winge himself declares to be anything but primitive<sup>1</sup>.

As the same author considers the Muridae to be a terminal group—and in this I certainly agree with him—I cannot see how we would have to explain the sudden appearance in them of a primitive molar form (that of *Cricetus*, according to Winge). All the other "*Cricetini*," in their more complicated molars, come nearer to the "*Anomaluridae*" than does *Cricetus*. *Pseudosciurus* and *Sciuroides* are considered by Winge himself to be the most primitive amongst *Anomaluridae*. Now the mesial "transverse ridge" is present in *Sciuroides* as well as in *Trechomys*, &c., although in the molars of the former it does not reach so far inwards (in upper molars) or outwards (in lower molars) as it does in *Trechomys*<sup>2</sup>.

#### Summary.

The Malagasy *Muridae* have, by common accord, been placed amongst the "*Cricetinae*" ("*Sigmodontinae*"); this is true in a general sense, at least with regard to the great majority of them.

In the foregoing pages I have tried to define more precisely their position, as well as their relationships with *Muridae* from other regions. Although the present paper deals essentially only with one genus, and though it will be necessary for me to take the Malagasy Rodents (forming, as I consider, a special subfamily, the *Nesomyiinae*) up again as a whole, when all the forms will have been fully worked out, I could not, for comparison's sake, avoid anticipating somewhat the future publication, by throwing side-glances on some of the other genera.

The Malagasy Rodents have to be considered as the lowest of the *Muridae*—lower even than the Miocene members of the family, so far as these are known,—because in cranial and dental characters they approach more than any other *Muridae* such more primitive groups of Rodentia as the *Dipodidae* and Winge's *Anomaluridae*. These characters are: large infraorbital foramen—well-developed jugale—absence of advanced hypselodontism—intermediate cusps of molars less reduced than in *Hesperomyiinae* and in Old World *Cricetinae*, and external cusps (of upper molars) less reduced than in the *Murinae*—greater agreement in pattern and size of m. 1 and m. 2 than in other *Muridae*; very often all three molars agree with each other.

If I had to regret that in my excavations I came upon but scanty remains of extinct fossil Mammalia, I have had some compensation by these *living* fossils. Were any justification necessary for having divided my time between neontological and palæontological exploration, this result would amply justify my proceeding.

<sup>1</sup> 'Jordfundne og nulevende Aber (Primates) fra Lagoa Santa, &c.,' Kjöbenhavn, 1895 ("E Museo Lundii"), p. 40. "Hvis Simiinerne's Kindtænder vare fremkomne af *Tænder saa lidt oprindelig som hos Cercopitheciner* . . ." (The italics are mine.)

<sup>2</sup> The comparison of the molars of *Sciuroides* with those of *Pseudosciurus* shows that the outer termination (in upper molars) of this "transverse ridge" is nothing but the ancient outer cusp, 2, of *Pseudosciurus*.



The light which the investigation of the Malagasy Rodentia has thrown on their relatives outside the Island has been somewhat unexpected to me. From what Peters had noted concerning the affinities of one of the genera <sup>1</sup> and from other considerations, I was prepared to meet with the nearest and perhaps the only close affinities amongst the American *Hesperomyinae*. These affinities certainly exist, and I have endeavoured to put them in their true light. However, other affinities, apart from those just mentioned, are very remarkable.

The genus *Brachytaromys*, which, as stated on a former occasion <sup>2</sup>, stands somewhat apart from the other Malagasy Rodents, proves to be a forerunner of the *Microtinae*. It is, however, certainly not a member of the genus *Microtus*, nor of any of the other genera included in the subfamily; it cannot even, in my opinion, be placed within this subfamily, for it lacks the specializations which characterize the latter. Apart from the molars being not only rooted, but even perfectly brachyodont, neither the last upper nor the first lower molar show any additional increase to the normal Muridine form; the skull, too, differs from the Microtine cranium in all the characters, which in these are the direct outcome of the increased vertical size of the molars and the adaptation to a subterranean life. But otherwise the teeth as well as the cranium (size and shape of the jugal, form of the rostrum, of the outer wall of the infraorbital foramen and of the foramen itself, general conformation of the upper region of the skull and its crests) are precisely such as we might expect them to have been in the forerunners of the *Microtinae*.

Next as to the genus *Nesomys*. The large size and breadth of the foramina incisivæ, and, what is still more to the point, the large size of the infraorbital foramen, and the strong development of the jugal—which characters this genus shares with most of the other Malagasy Rodents—show it to be a very low member of the *Muridæ*, approaching the *Dipodidæ*. The two anterior molars, agreeing in size and general form with each other, tell the same tale. The intimate structure of the molars, as compared with the *Hesperomyinae* and the *Murinae*, might induce us to consider *Nesomys* as a connecting-link between these two groups. But the relationship to them will be more rightly expressed by considering it to be ancestral to both; especially if we bear in mind that the characters of both the cranium and teeth are less specialized than in the two subfamilies mentioned.

The present paper deals chiefly with a third genus, *Brachyuromys*. Its affinities with some fossorial Rodents, viz. *Tachyoryctes* from Abyssinia, *Rhizomys* from the Oriental Region, *Spalax* and *Siphneus* from the Palæarctic, have been fully discussed, and as one of the results these four genera are classed amongst the lowest *Muridæ*. Retirement under the earth and adaptation to fossorial habits have done for these four genera what isolation has done for

<sup>1</sup> Sitzungsber. Ges. naturf. Freunde Berlin, Oct. 18, 1870, pp. 54, 55. See also P. Z. S. 1896, p. 978.

<sup>2</sup> P. Z. S. 1896, p. 979.

*Brachyuromys* &c., i. e. the preservation of primitive types of *Muridæ*<sup>1</sup>. There is a parallel to that of the African insectivorous family *Chrysochloridæ*, as compared with the more generalized members of the Malagasy family *Centetidæ*.

Whilst the somewhat closer agreement with *Brachyuromys* thau with the rest of Malagasy Rodents may in the case of *Rhizomys*, *Spalax*, and *Siphneus* be due to the circumstance that in each the molars are hypselodont (though in a much lesser degree in *Brachyuromys*), the case seems to be different with regard to *Tachyoryctes*. This latter is in the pattern of its molars almost identical with one of the species of *Brachyuromys* (*B. ramirohitra*).

The mutual relations of the *Hesperomyiinae*, *Microtinae*, *Murinae*, and *Spalacidæ* with each other and with the Malagasy *Nesomyiinae* have thus to a certain extent been cleared up by a better acquaintance with the latter.

#### EXPLANATION OF THE PLATES.

##### PLATE XXXVII.

- Fig. 1. Skull of *Brachyuromys betsileoensis* (Bartl.): fig. 1, side view; 1 a, from below; 1 b, from above; 1 c, front view.  
 2. Skull of *B. ramirohitra*, Maj.: fig. 2, side view; 2 a, from below; 2 b, from above; 2 c, front view; 2 d, side view of mandible.  
 3. Skull of *Tachyoryctes splendens*, Rüpp.: fig. 3, side view; 3 a, from below; 3 b, from above; 3 c, front view.  
 All figures nat. size.

##### PLATE XXXVIII.

- Different views of the skull of *Rhizomys sinensis*, Gray. Nat. size. Fig. 1, side view; fig. 2, from above; fig. 3, from below; fig. 4, from behind; fig. 5, oblique view of left infraorbital foramen; fig. 6, postero-superior part of left mandible, from behind.

##### PLATE XXXIX.

- Figs. 1 a-8 a. Upper molars of *Brachyuromys* and *Tachyoryctes*, enlarged.  
 1 b-8 b. Lower molars of ditto.  
 1 a-3 b. *Brachyuromys ramirohitra*, Maj.  
 4 a-4 b. *Tachyoryctes annectens*, Thos.  
 5 a-6 b. *T. splendens*, Rüpp.  
 7 a-8 b. *Brachyuromys betsileoensis* (Bartl.).

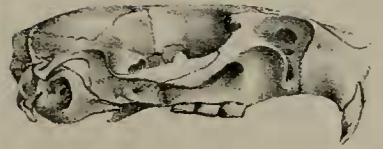
##### PLATE XL.

- Figs. 1 a-7 a. Upper molars of various species of *Rhizomys*, enlarged.  
 1 b-9 b. Lower molars of ditto.  
 1 a-3 b. *Rhizomys badius*, Hodgs.  
 4 a, 4 b. *R. pruinusosus*, Blyth.  
 5 a-6 b. *R. sumatrensis* (Raffles).  
 7 a-8 b. *R. sinensis*, Gray.  
 9 b. *R. sivalensis*, Lyd.

<sup>1</sup> Still more striking instances amongst Rodentia of adaptation as a preserver of primitive types are afforded by the *Aplodontidæ* and the *Leporidæ*, both of them very primitive Rodent families showing the curious combination of some very specialized features with their primitive characters.



1.



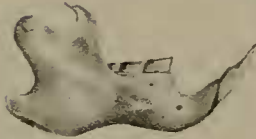
2.



3.



3 c.



2 d.



1 a.



3 a.



2 a.



1 c.



2 c.



1 b.



3 b.



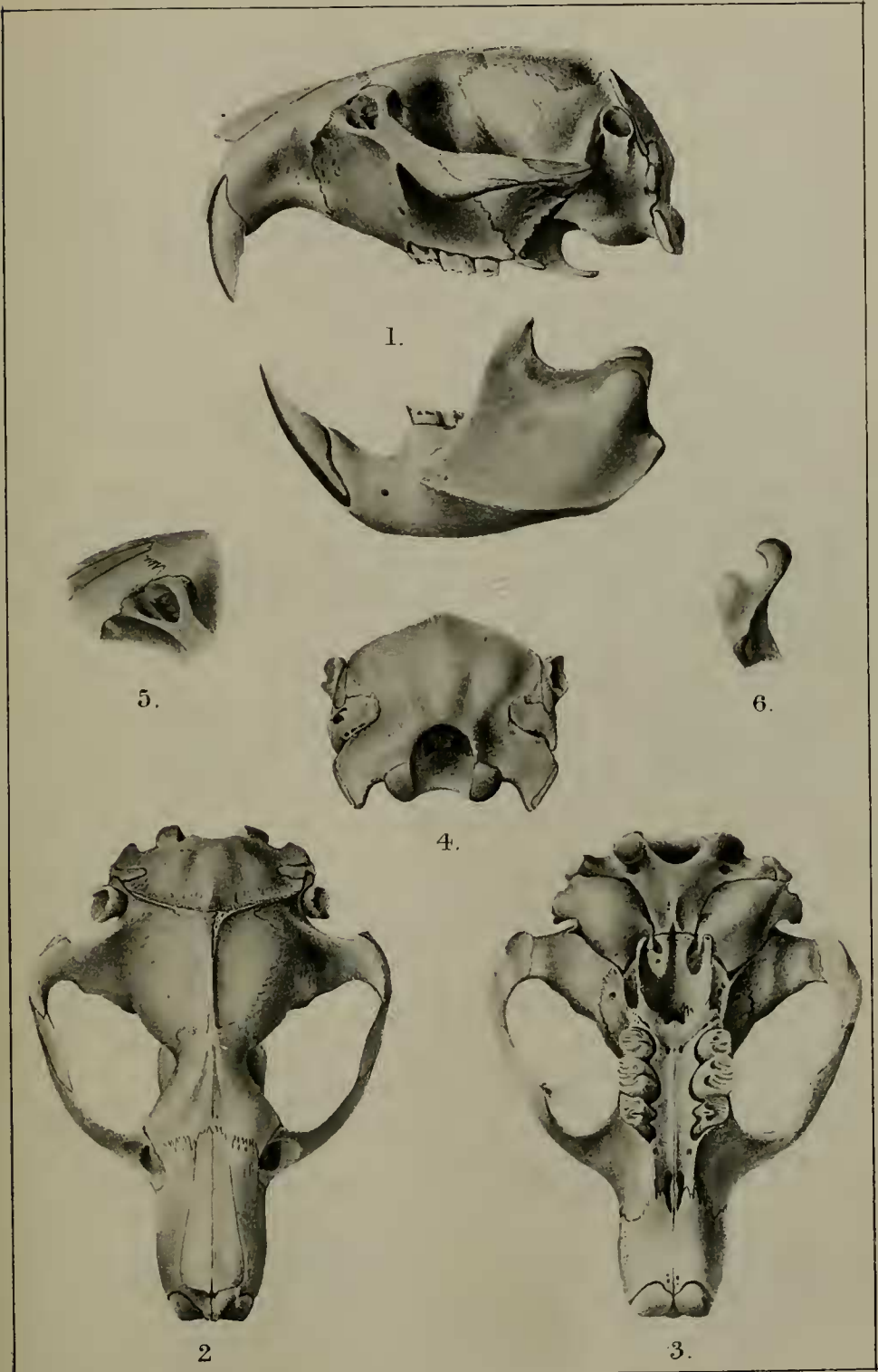
2 b.

H. Gronvold del. et lith.

Mirdern Bros. imp.

1. BRACHYUROMYS BETSILEOENSIS. 2. B. RAMIROHITRA.

3. TACHYORYCTES SPLENDENS.



SKULL OF RHIZOMYS SINENSIS.

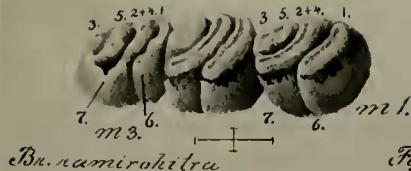


Fig. 1a *Br. ramirohitra.*

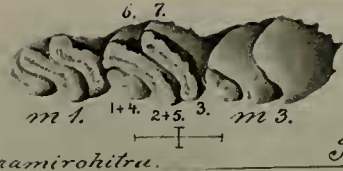


Fig. 1b.

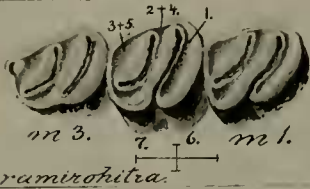


Fig. 2a

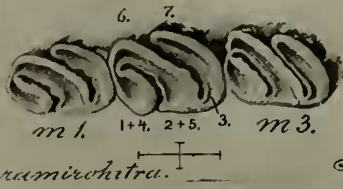


Fig. 2b.



Fig. 3a

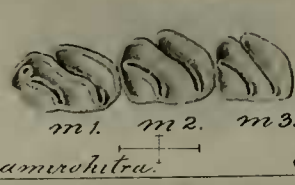


Fig. 3b.

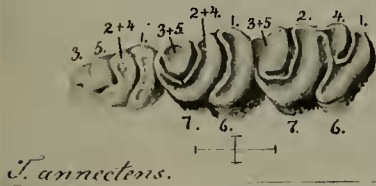


Fig. 4a



Fig. 4b.

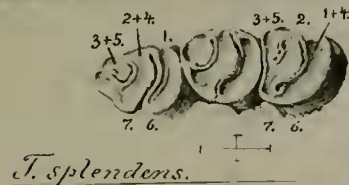


Fig. 5a



Fig. 5b.

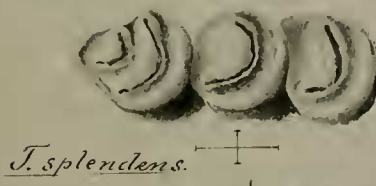


Fig. 6a

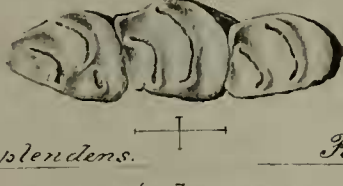


Fig. 6b.

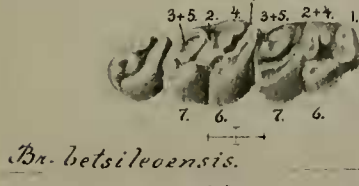


Fig. 7a

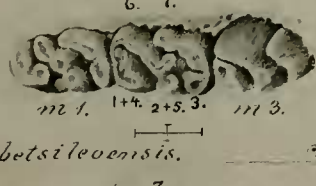


Fig. 7b.

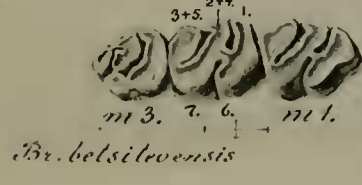


Fig. 8a

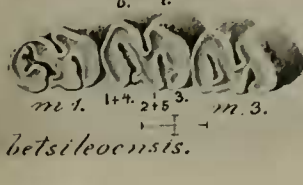
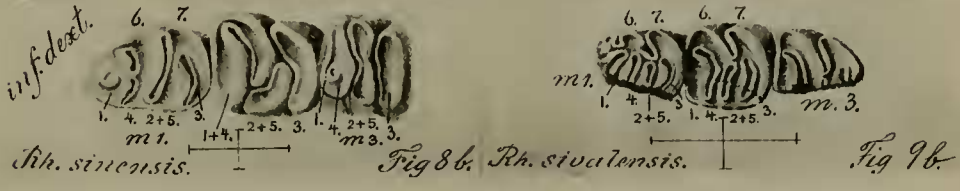
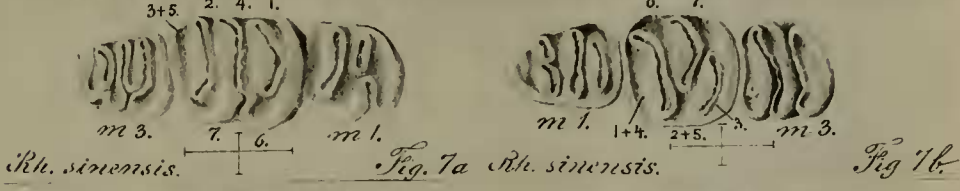
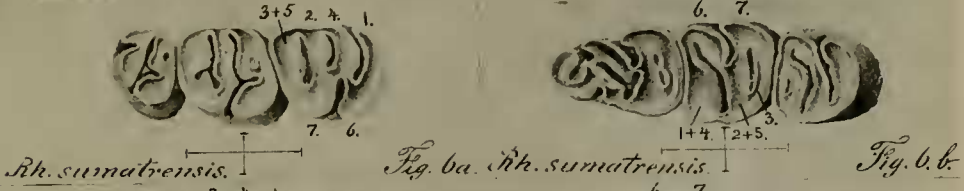
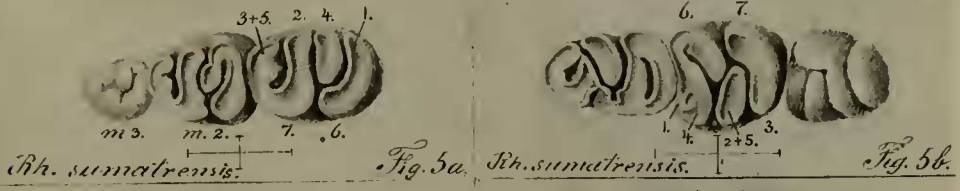
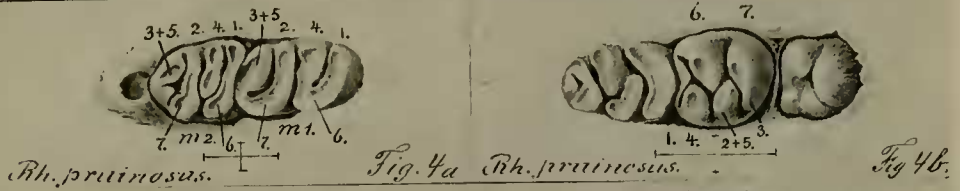
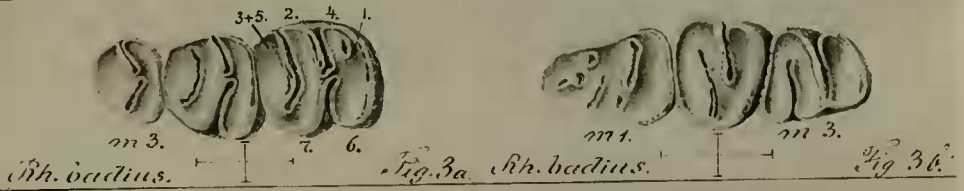
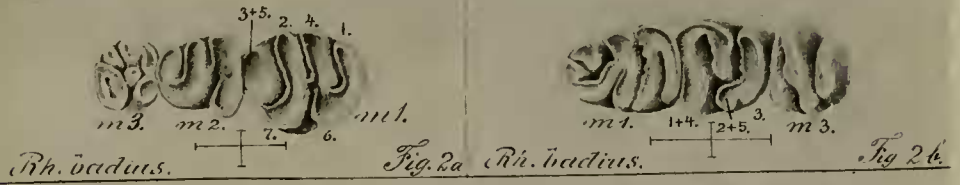
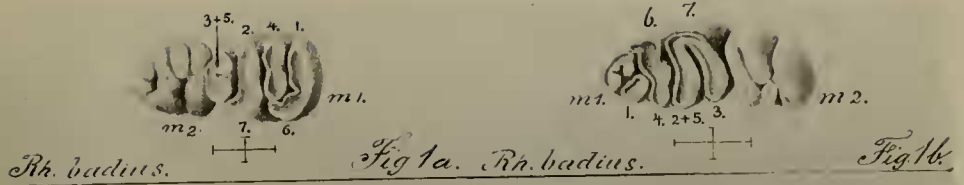


Fig. 8b.



Enlarged upper and lower molar teeth of recent and fossil SPECIES OF RHIZOMYS.